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STUDIES ON CAVE HARVESTMEN OF THE CENTRAL SIERRA NEVADA WITH DESCRIPTIONS OF NEW SPECIES OF *BANKSULA*

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ABSTRACT: New ecological and biogeographic information on Sierra Nevada cave harvestmen in *Banksula* was obtained while environmental impact and mitigation work was being done for the Army Corps of Engineers New Melones Dam project. Isolation appears to be the principal factor leading to speciation in *Banksula*, but the distribution of species in the vicinity of the New Melones Reservoir is not readily explained. Four new species of *Banksula* are described: *B. rudolphi*, *B. martinorum*, *B. grubbsi*, and *B. elliotti*.

Introduction

Troglobitic organisms are scarce in California caves, possibly due to the relatively small size and geologic youth of these habitats. Laniatorid harvestmen of the genus *Banksula* are distinctive because they are relatively abundant obligate cavernicoles of the Calaveras Formation of the Sierra Nevada. Intensive collecting by biospeleological investigators contracted by the Army Corps of Engineers, the Fish and Wildlife Service, and the Office of Endangered Species has yielded numerous new records and four new species of *Banksula*. Project teams worked primarily in the vicinity of the New Melones Reservoir site on the Stanislaus River, Calaveras and Tuolumne counties, where several caves are threatened by completion of the New Melones Dam. Biological surveys were begun in May 1975 when a mine tunnel in limestone was selected for transplanting biota, including *Banksula grahami* and *B. melones*, from McLean's Cave, the largest of the threatened caves. As additional workers transplanted animal and plant life from McLean's Cave and studied other nearby caves, some distributional, behavioral, and ecological information were obtained which allow us to present some biogeographic discussion of *Banksula*.

Briggs (1974) reviewed and expanded the genus *Banksula* and described four species with functional eyes. He showed that the single previously known species, *Banksula californica* (Banks), lacked corneas and retinae. His contention that all *Banksula* are confined to caves is supported by all subsequent investigations. Only *Banksula melones*, which has relatively

well-developed eyes, has been collected near or at the cave twilight zone. *Sitalcina sierra* Briggs and Hom is the only laniatorid harvestman found in epigean habitats adjacent to cave localities.

Methods and Deposition

The structures measured and morphological terminology used in this paper are generally those described by Briggs (1968) for laniatorid harvestmen, with one modification that appears in this paper and in Briggs (1974): we substitute "second endites" for that portion of the second coxae previously referred to as the maxillary processes. Another structure, the labial process, first described by Briggs (1971), is located between the second endites.

Unless otherwise noted, all specimens recorded in this paper were preserved in ethyl alcohol and are deposited in the collection of the California Academy of Sciences.

Key to the Species of *Banksula*

1a. Operculum small, held almost entirely between mesal margins of fourth coxae; males with apex of aedeagus not enclosed in sheath, velum on dorsal plate smooth (*californica* group) 2

1b. Operculum large, with posterior margin well behind mesal extreme of posterior margin of fourth coxae; males with apex of aedeagus enclosed in sheath, velum on dorsal plate in transverse folds (*melones* group) 7

2a. Retinae entire; eye tubercle obliquely truncate in lateral view ..... *B. galilei* Briggs

2b. Retinae absent or incomplete; if retinae present, eye tubercle a rounded cone 3

3a. Small spines or tubercles between principal dorsal spines on palpal femur; corneas absent ..... *B. californica* (Banks)

3b. No small spines or tubercles between principal dorsal spines on palpal femur; corneas present or absent 4

4a. Proximal ventral spinose tubercle on palpal tibia equal to ventral spinose tubercle on patella; retinae absent; corneas present or absent 5

4b. Proximal ventral spinose tubercle on palpal tibia always smaller than ventral spinose tubercle on patella; retinae incomplete or absent; corneas present 6

5a. Submarginal row of tubercles on eighth tergite and last sternite ..... *B. rudolphi* new species

5b. No submarginal rows of tubercles on tergites or sternites ..... *B. martinorum* new species

6a. Eye tubercle a rounded cone; small spur ectal to proximal ventral spine on palpal femur; incomplete retinae usually present ..... *B. tuolumne* Briggs

6b. Eye tubercle obliquely truncate in lateral view; no spur ectal to proximal ventral spine on palpal femur; retinae absent ..... *B. grubbsi* new species

7a. First legs longer than 4 mm; retinal diameter greater than 0.03 mm; aedeagus and enclosing sheath fold anterior to recurved prongs of dorsal plate ..... *B. melones* Briggs

7b. First legs shorter than 4 mm; retinal diameter less than 0.03 mm or missing; aedeagus and enclosing sheath held within bifurcate dorsal plate 8

8a. Eye tubercle and elevated area behind without tubercles; retinae present ..... *B. grahami* Briggs

8b. Eye tubercle and elevated area behind tuberculate; retinae reduced or missing ..... *B. elliotti* new species

Banksula rudolphi new species

(Figure 2)

Holotype.—Male. Body length 1.67 mm; scute length 1.40 mm; scute width 1.14 mm; eye tubercle length 0.23 mm; eye tubercle width 0.28 mm; operculum length 0.18 mm; operculum width 0.21 mm.

Palp: trochanter 0.19 mm, femur 0.79 mm, patella 0.44 mm, tibia 0.65 mm, tarsus 0.44 mm.

Leg II: trochanter 0.19 mm, femur 1.42 mm, patella 0.44 mm, tibia 1.26 mm, metatarsus 1.02 mm, tarsus 1.58 mm.

Scute with segmentation delineated by tubercles, eye tubercle and area behind tuberculate. Eye tubercle a rounded cone without retinae (some individuals also without corneas). Tergites with row of tubercles at margin, eighth tergite also with medial row of tubercles. Posterior

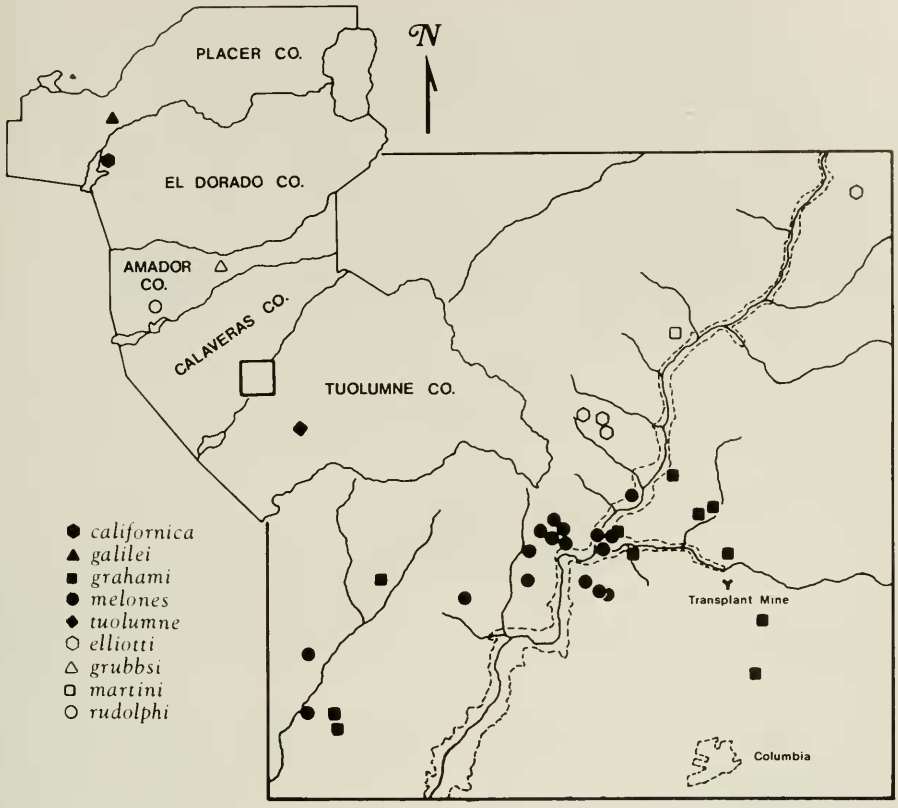

FIGURE 1. Map showing counties in the central Sierra Nevada where *Banksula* have been collected. The inset shows the region along the Stanislaus River where environmental impact and mitigation work on *Banksula* has been concentrated.

sternite with two rows of tubercles. Anal plate with medial tubercles. Second endites with concave ectal margin. Labial processes rounded. Operculum with narrow, rounded anterior; posterior margin adjacent to mesal extreme of posterior margin of fourth coxae.

Palpal femur with six prominent proximal dorsal spines (some individuals with only five spines) and one small distal dorsal spine; no setae or tubercles between dorsal spines; ectal spur at base of first ventral spine small and rounded; venter with numerous small tubercles. Proximal ventral tubercle on palpal tibia reduced, spine from tubercle absent. Ventral spine on palpal patella arising from a reduced tubercle.

Tarsal formula 4-6-5-6.

Body concolorous yellow-orange.

Penis typical of *californica* group (see Briggs 1974:11–12).

ALLOTYPE.—Female. Slightly smaller than holotype. Proximal ventral spinose tubercle on palpal tibia present, equal in size to robust ventral spinose tubercle on palpal patella. Operculum with truncate apex (rounded in some individuals); posterior margin behind mesal extreme of posterior margin of fourth coxae.

TYPE-SPECIMENS.—Holotype, allotype, 21 paratypes (9 ♂, 9 ♀, 3 juv.): Chrome Cave, near Jackson, Amador County, California, 5 Apr. 1979, D. C. Rudolph, S. Winterath, and B. Martin. Paratypes, 2 ♂, 2 ♀, 3 juv.: same locality, 21 Sep. 1980, T. S. Briggs and D. Ubick. Paratype, 1 ♂: same locality, 24 Jan. 1981, T. S. Briggs and D. Ubick.

ETYMOLOGY.—This species is named for biospeleologist D. Craig Rudolph.

ECOLOGICAL NOTES.—Chrome Cave is a small cave situated in about 0.02 km² of limestone. The outcrop is surrounded by serpentine which also forms much of the cave's walls. The humidity is relatively high and a mean temperature of 18 C was recorded on 24 January 1981. *Bank-*

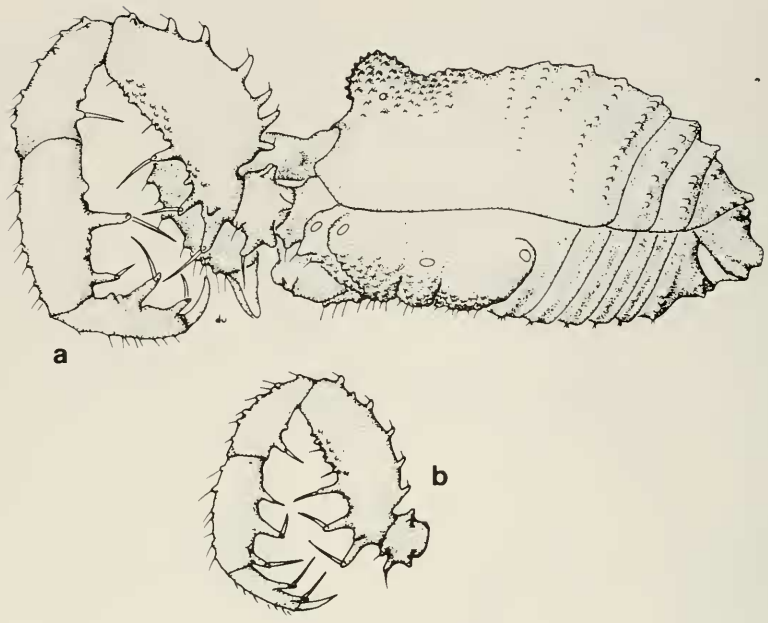

FIGURE 2. *Banksula rudolphi* Briggs and Ubick, new species. *a*. Lateral view of body and left palpus of male holotype; *b*. Lateral view of left palpus of female allotype.

sula rudolphi is found throughout the upper regions of the cave, predominantly on the undersides of rocks. Associated with *Banksula* is a rich assortment of predators, of which spiders (Araneae) are most abundant. We recorded the following species: *Archoleptoneta schusteri* Gertsch, *Liocranoides* sp., *Trogloneta paradoxa* Gertsch, and *Usofila* (*Telema*) sp. Of the other cavernicoles encountered, the most interesting were specimens of *Prokoenenia* sp. (Palpigradida).

Banksula martinorum new species
(Figure 3)

HOLOTYPE.—Male. Body length 1.75 mm; scute length 1.49 mm; scute width 1.23 mm; eye tubercle length 0.26 mm; eye tubercle width 0.33 mm; operculum length 0.18 mm; operculum width 0.19 mm.

Palp: trochanter 0.19 mm, femur 0.88 mm, patella 0.53 mm, tibia 0.65 mm, tarsus 0.42 mm.

Leg II: trochanter 0.21 mm, femur 1.81 mm, patella 0.39 mm, tibia 1.67 mm, metatarsus 1.23 mm, tarsus 2.37 mm.

Scute with segmentation delineated by small tubercles; eye tubercle and area behind slightly tuberculate. Eye tubercle subconical, without retinae or corneas. Tergites with submarginal row of tubercles. Second endites large, ectal margin slightly concave. Labial processes with acute anterior margin. Operculum with rounded anterior, posterior margin slightly behind mesal extreme of posterior margin of fourth coxae. First coxae with two prominent spinose tubercles. Anal plate smooth.

Palpal femur with five prominent proximal dorsal spines and two slightly smaller distal dorsal spines; no setae or tubercles between dorsal spines; ectal spur at base adjacent to second ventral spine. Proximal ventral spinose tubercle on palpal tibia equal to ventral spinose tubercle on patella.

Tarsal formula 4-6-5-6.

Body concolorous pale yellow.

Penis typical of *californica* group.

ALLOTYPE.—Female. Similar to male.

TYPE-SPECIMENS.—Holotype, allotype, 3 paratypes (1 ♀, 2 juv.): Heater Cave, 8 km N Columbia, Calaveras County, California, 15 Mar. 1979, D. C. Rudolph, B. Martin, and S. Winterath.

ETYMOLOGY.—This species is named for arachnologist Barbara Martin and for Army Corps of Engineers environmental planner Robert Martin.

FIGURE 3. *Banksula martinorum* Briggs and Ubick, new species. Lateral view of body and left palpus of male holotype.

Banksula grubbsi new species
(Figure 4)

HOLOTYPE.—Male. Body length 1.49 mm; scute length 1.26 mm; scute width 1.23 mm; eye tubercle length 0.25 mm; eye tubercle width 0.35 mm; operculum length 0.18 mm; operculum width 0.21 mm.

Palp: trochanter 0.19 mm, femur 0.70 mm, patella 0.39 mm, tibia 0.53 mm, tarsus 0.65 mm.

Leg II: trochanter 0.18 mm, femur 1.49 mm, patella 0.44 mm, tibia 1.23 mm, metatarsus 0.96 mm, tarsus 1.49 mm.

Scute with segmentation delineated by small tubercles, area behind eye tubercle tuberculate. Eye tubercle obliquely truncate, declining posteriorly; entire surface tuberculate. Eyes with small corneas and no retinae. Tergites with submarginal row of tubercles. Second endites setose, with acute ectal invagination behind midpoint. Labial processes large, rounded. Small operculum with rounded anterior, margin adjacent to fourth coxae, posterior margin slightly behind mesal extreme of posterior margin of fourth coxae.

Chelicerae setose, only slightly tuberculate.

Palpal femur with four prominent proximal dorsal spines and three reduced distal dorsal spines; no setae or tubercles between proximal dorsal spines; ectal spur at base replaced by a broad, low tubercle; ventral margin straight. Palpal tibia without significant proximal ventral spine.

Tarsal formula 4-6-5-6.

Body concolorous light yellow.

Penis typical of *californica* group, aedeagal velum held in smooth dorsal plate.

TYPE-SPECIMEN.—Holotype: Black Chasm Cave, near Volcano, Amador County, California, 19 Feb. 1978, A. G. Grubbs.

FEMALE.—Unknown.

ETYMOLOGY.—This species is named for biospeleologist Andrew G. Grubbs.

Banksula elliotti new species
(Figure 5)

HOLOTYPE.—Male. Body length 1.61 mm; scute length 1.23 mm; scute width 1.28 mm; eye tubercle length 0.26 mm; eye tubercle width 0.35 mm; operculum length 0.30 mm; operculum width 0.32 mm.

Palp: trochanter 0.23 mm, femur 0.63 mm, patella 0.39 mm, tibia 0.53 mm, tarsus 0.39 mm.

Leg II: trochanter 0.16 mm, femur 1.14 mm, patella 0.35 mm, tibia 0.96 mm, metatarsus 0.72 mm, tarsus 1.14 mm.

Scute with segmentation delineated by tubercles, eye tubercle and area behind tuberculate. Eye tubercle rounded, slightly conical, with small corneas and without retinae. Tergites with row of tubercles at margin. Second endites setose, mesally broad and rounded; labial processes spatulate. Operculum large, extending posterior to hind coxae. Hind sternite and anal plate with row of tubercles. All coxae tuberculate.

Chelicerae with strongly tuberculate anterior margin.

Palpal femur with six prominent proximal dorsal spines and four reduced distal dorsal spines; no setae or tubercles between proximal dorsal spines; ectal spur well developed at base of

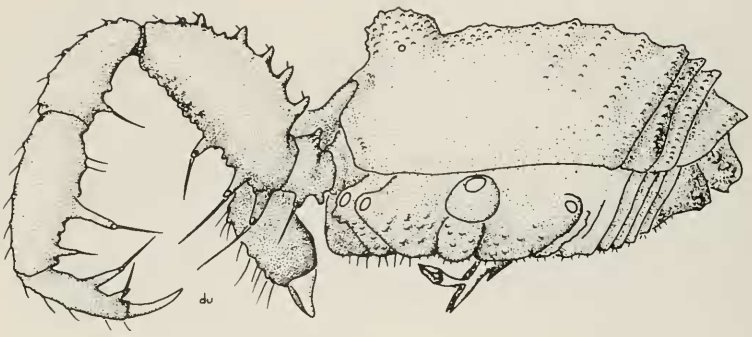

FIGURE 4. *Banksula grubbsi* Briggs and Ubick, new species. Lateral view of body and left palpus of male holotype.

proximal ventral spine, ventral surface tuberculate.

Tarsal formula 4-6-5-6.

Body concolorous yellow-orange.

Penis with folds at base of dorsal plate; apex of aedeagus enclosed in rounded sheath and held within distal bifurcation of dorsal plate.

ALLOTYPE.—Female. Similar to male.

TYPE-SPECIMENS.—Holotype, allotype, 4 paratypes (2 ♂, 1 ♀, 1 juv.): Pinnacle Point Cave, near Camp Nine Power House, 9.6 km N Columbia, Tuolumne County, California, 8 Feb. 1979, D. C. Rudolph, B. Martin, and S. Winterath. Paratypes, 2 ♂, 2 juv.: same locality, 20 Jan. 1978, W. Elliott, A. Grubbs, and S. Winterath. Paratypes, 2 ♂, 1 ♀: same locality, 1 May 1977, A. Grubbs, N. Boice, M. McEachern and J. Davis. Paratypes, 1 ♀: Digger Pine Cave, 6.5 km N Columbia, Calaveras County, 22 Mar. 1979, D. Rudolph, B. Martin, S. Winterath, W. Elliott, and J. Reddell. Paratypes, 3 ♂, 5 ♀: Rabbit Hole Cave, 6.5 km N Columbia, Calaveras County, 22 Mar. 1979, D. Rudolph, B. Martin, and S. Winterath. Paratypes, 1 ♂, 1 ♀: Grapevine Gulch Cave, 6.5 km N Columbia, Calaveras County, 22 Nov. 1979, D. Rudolph, B. Martin, and S. Winterath. Paratypes, 1 ♂, 4 ♀: same locality, 27 Apr. 1977, B. Hawson, A. Grubbs, J. Munthe, and M. McEachern.

ETYMOLOGY.—This species is named for biospeleologist William R. Elliott.

VARIATIONS.—Specimens taken in Pinnacle Point Cave are without retinae, although half of the specimens taken in the remaining caves have retinal pigment in their eyes. The specimen from Digger Pine Cave has a relatively more conical eye tubercle. Some specimens have only three distal dorsal spines on the palpal femur.

Banksula grahami Briggs

Banksula grahami BRIGGS 1974:7.

RECORDS.—*Calaveras County:* Moaning Cave, near Vallecitos, 22 Aug. 1963, 22 Dec. 1968, 6 Dec. 1977, R. Graham, T. Briggs, W. Elliott, A. Grubbs, and S. Winterath; Linda's Cave, 6 km W Columbia, 16 May 1977, A. Grubbs, N. Boice, and D. Broussard; Carlow's Cave, 6 km W Columbia, 16 May 1977, A. Grubbs, N. Boice, and D. Broussard. *Tuolumne County:* Experimental Mine Cave, 3 km N Columbia, 25 Jun. 1975, R. Lem; Mine tunnel along road to Experimental Mine, 2.5 km N Columbia, 25 Jun. 1975, T. Briggs (identification only); Snell's Cave, 3 km N Columbia, 26 Feb. 1978, 14 Feb. 1978, 2 Apr. 1979, S. Winterath, D. Rudolph, and J. Reddell; Crystal Palace Cave, 5 km N Columbia, 4 Nov. 1967, 21 Dec. 1977, 4 Feb. 1979, 25 Mar. 1979, T. Briggs, V. Lee, D. Rudolph, S. Winterath, A. Grubbs, W. Elliott, B. Martin, and J. Reddell; Porcupine Cave, 5 km N Columbia, 4 Feb. 1979, 28 Feb. 1979, D. Rudolph, S. Winterath, and B. Martin; mine on ridge, 4.5 km N Columbia, 22 Feb. 1979, D. Rudolph, S. Winterath, and B. Martin; Banksula Cave, 6 km N Columbia, 21 Mar. 1979, D. Rudolph, B. Martin, S. Winterath, and W. Elliott; McLean's Cave, 4.5 km N Columbia, 13 May 1967, 14 Dec. 1977, 18 Dec. 1977, 6 Mar. 1979, 27 Mar. 1979, 2 Apr. 1979, K. Hom, T. Briggs, W. Elliott, A. Grubbs, S. Winterath, D. Rudolph, and B. Martin; Transplant Mine, 3 km N Columbia, 17 Apr. 1979, D. Rudolph, S. Winterath, and E. vanIngen.

NOTES.—The migration of *Banksula grahami* into two of the mine tunnels recorded above is the only known example of probable interstitial movement by a species of *Banksula*.

Banksula melones Briggs

Banksula melones BRIGGS 1974:8.

RECORDS.—*Calaveras County:* Cave of Skulls, 5 km NW Columbia, 16 Apr. 1977, 29 Mar. 1979, T. Briggs, D. Rudolph, B. Martin, S. Winterath, W. Elliott, and J. Reddell; Quail (Gerritt's) Cave, 5 km NW Columbia, 3 Jul. 1975, 17 Apr. 1977, 30 Mar. 1979, W. Rauscher, D. Cowan, B. Martin, and S. Winterath; Barren Cave, 5 km NW Columbia, 30 Mar. 1979, D. Rudolph, B. Martin, S. Winterath, W. Elliott, and J. Reddell; Beta Cave, 5 km NW Columbia, 7 May 1977, 29 Mar. 1979, A. Grubbs, D. Broussard, S. Winterath, D. Rudolph, W. Elliott, J. Reddell, and B. Martin; Poison Oak Cave, 5 km NW Columbia, 29 Mar. 1979, D. Rudolph, B. Martin, S. Winterath, W. Elliott, and J. Reddell; Coral Cave, 5 km N Columbia, 24 Feb. 1978, 22 Mar. 1979, A. Grubbs, D. Rudolph, B. Martin, S. Winterath, W. Elliott, and J. Reddell; Bryden's Cave, 5 km NW Columbia, 29 May 1977, A. Grubbs and B. Hopkins; Cone Cave, 5 km NW Columbia, 30 Mar. 1979, D. Rudolph, B. Martin, S. Winterath, W. Elliott, and J. Reddell; Eagle View Cave No. 2, 5 km NW Columbia, 29 Mar. 1979, D. Rudolph, B. Martin, S. Winterath, W. Elliott, and J. Red-

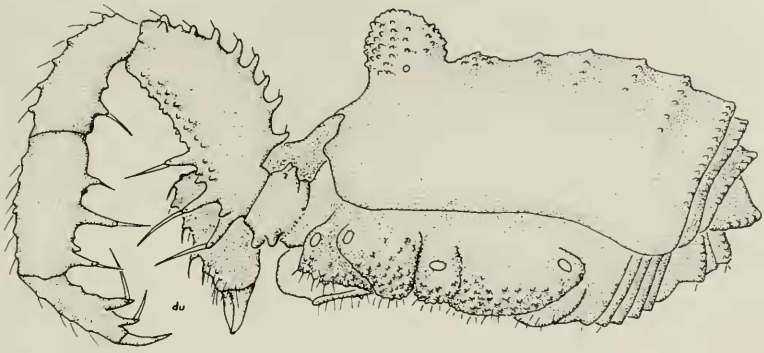

FIGURE 5. *Banksula elliotti* Briggs and Ubick, new species. Lateral view of body and left palpus of male holotype.

dell; Lost Piton Cave, 6.5 km W Columbia, 6 May 1977, 26 Mar. 1979, A. Grubbs, N. Boice, D. Broussard, S. Winterath, W. Elliott, and J. Reddell; Bone Cave, 6 km W Columbia, 20 Apr. 1980, T. Briggs and D. Ubick. *Tuolumne County:* Quarry (McNamee's) Cave, 3 km NW Columbia, 24 May 1969, G. Leung, W. Rauscher, and T. Briggs; Gate Pit Cave, 3 km NW Columbia, 1 Apr. 1979, D. Rudolph; Mine Cave, 3 km NW Columbia, 1 Apr. 1979, D. Rudolph, B. Martin, and S. Winterath; Scorpion Cave, 4.5 km N Columbia, 8 Feb. 1979, 25 Mar. 1979, D. Rudolph, S. Winterath, D. Cowan, and T. Briggs; Vulture Cave, 4.5 km N Columbia, 10 Feb. 1979, 17 Feb. 1979, 22 Feb. 1979, 19 Mar. 1979, S. Winterath, D. Rudolph, B. Martin, and W. Elliott; McLean's Cave, 4.5 km N Columbia, 13 May 1967, 17 June 1967, 24 June 1967, 14 Dec. 1977, 18 Dec. 1977, 6 Mar. 1979, 27 Mar. 1979, K. Hom, T. Briggs, V. Lee, W. Elliott, A. Grubbs, S. Winterath, D. Rudolph, and B. Martin; Transplant Mine, 3 km N Columbia, 17 Apr. 1979, D. Rudolph, S. Winterath, and E. vanIngen.

NOTES.—Some of the specimens collected in Vulture Cave and Bone Cave were found under rocks in the twilight zone. All other collections were made in permanently dark regions of caves.

ECOLOGICAL REVIEW

Several ecological studies on *Banksula* (Briggs 1975; Elliott 1978; Rudolph 1979) have been conducted in McLean's Cave at the confluence of the Middle Fork and the South Fork of the Stanislaus River (approximate elevation, 300 m). This cave is one of the largest in the Calaveras limestone of the central Sierra Nevada and contains the only sympatric populations of *Banksula* species. *Banksula melones* and *B. grahami* are mixed in habitats near the base of a broad talus cone formed by debris gradually moving through two small entrances to the lowest levels of the cave. Because there is no flowing water in the cave, the talus cone and deep-penetrating roots are important food sources for the inhabitants. The cave temperature ranges from 14 C to 16 C and the humidity from 82% to 97% (Elliott 1978). Specimens of *Banksula melones* and *B. grahami* were found under rocks or wandering on the floor or walls. They were rarely captured in baited pitfall traps (Briggs 1975; Elliott 1978). Although biased by more intensive winter collecting, records from McLean's and other caves suggest greatest activity in winter and spring.

At least 30 species of arthropods, most of which were listed by Elliott (1978), coexist with *Banksula melones* and *B. grahami* in McLean's Cave. Elliott (1978) identified some species, but many have not yet been identified. His feeding experiments showed that captive *Banksula*, kept in McLean's Cave, will eat live Collembola but not equally abundant Psocoptera. Rudolph (1979) maintained eight immature *Banksula* in McLean's Cave using Collembola as food; three molted within 43 days. One adult and two immature individuals maintained at the same time without food survived.

Rudolph (1979) searched the mine tunnel into which Briggs and Elliott transplanted *Banksula melones, B. grahami,* and miscellaneous arthropods from McLean's Cave. The transplanted population, which included a few hundred *Banksula*, appeared to be reproducing. The future of this transplant may depend on how well conditions in the mine duplicate conditions in McLean's Cave. If they both flourish, the transplanted *Banksula* species may demonstrate that their sympatry in a small cave is stable.

BIOGEOGRAPHY

The distribution of *Banksula* species is similar to the invertebrate troglobite distributions reported from caves in the Appalachian Mountains

of the eastern United States in that these cave species tend to be bounded within "karst islands," within which subterranean dispersal and genetic communication readily occurs (Barr 1967; Culver et al. 1973). Such karst-island speciation exists for *Banksula* in the Sierra Nevada if the limestone outcrops are widely separated. Thus, the species *B. galilei* Briggs, *B. californica* (Banks), *B. rudolphi* new species, *B. grubbsi* new species, and *B. tuolumne* Briggs occupy karst that is separated by many kilometers of nonporous rock (Fig. 1). The isolation of these cave species is, therefore, more complete than that of the species in the Appalachian caves. The area of the karst in which *B. galilei*, *B. californica*, and *B. rudolphi* are found is 0.02–0.1 km² and is considerably smaller than the smallest karst island (10 km²) studied in the eastern United States (Culver et al. 1973). Furthermore, quarrying shows that these small outcrops have small volume and little internal water flow.

All known *Banksula* species are allopatric except for *B. melones* and *B. grahami* in McLean's Cave. This suggests that sympatric species compete, and the sympatry in McLean's Cave is a result of a recent invasion. About half of the 70 or so Calaveras Formation caves carefully checked yielded a species of *Banksula*. Thirty-one of these are located in the karst of the Stanislaus River. Eighteen apparently habitable caves in this region did not contain *Banksula* (Rudolph 1979). The absence of harvestment in caves located in karst outside of the Stanislaus River region may be due to an uneven distribution of their epigean ancestors.

The distribution of the four species of *Banksula* (*B. melones*, *B. grahami*, *B. martinorum*, and *B. elliotti*) that occupy the karst of the Stanislaus region is not readily explained. Volcanic rock divides Coyote Creek (west of the Stanislaus River) from the Stanislaus River. It forms an irregular barrier between *B. elliotti* and *B. melones*, and separates *B. melones* from *B. grahami* southeast of the Stanislaus River. Several continuous bands of amphibolite divide the remaining limestone regions into parallel lenses in which allopatric populations of *B. melones* and *B. grahami* occupy most of the available caverns. These populations seem to split into eastern and western clusters that do not correlate well with geology or water systems. The karst that contains the easternmost population of *B. elliotti* is isolated by one kilometer of metavolcanic rock from the karst that contains the rest of *B. elliotti* and *B. martinorum*. Coyote Creek, the much larger Stanislaus River, and the south fork of the Stanislaus that branches to the east have no apparent effect on the distribution of species of *Banksula*. The four Stanislaus species show increasing cavernicolous specialization in relative eye loss, from *B. melones* with the largest eyes, to *B. elliotti* with missing retinae, and *B. martinorum* with complete eye loss. One might infer that adaptive radiation began with a *B. melones*-like ancestor and progressed to *B. elliotti*. If correct, one must explain how the increasingly troglobitic species *B. grahami* and *B. elliotti* were able to cross geologic and drainage barriers. Further studies on the harvestmen of the Stanislaus River region are needed to explain this unexpected distribution of species. It is regrettable that this portion of the river will soon be inundated by the New Melones Reservoir and some of the harvestmen caves will be lost.

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